

STUDIES ON *DOMECIA ACANTHOPHORA*, A COMMENSAL CRAB FROM PUERTO RICO, WITH PARTICULAR REFERENCE TO MODIFICATIONS OF THE CORAL HOST AND FEEDING HABITS

WENDELL K. PATTON

Ohio Wesleyan University, Delaware, Ohio 43015

In the summer of 1965, a survey was made of the fauna of living portions of *Acropora* colonies at La Parguera, on the south coast of Puerto Rico. Collections and underwater observations were made in shallow depths (0-10 feet) at the west end of Enrique Reef. This region has good coral growth but less wave action than the southern, seaward face of the reef (Almy and Carrión-Torres, 1963). Contrary to my expectations, the xanthid crab *Domecia acanthophora* (Desbonne and Schramm) was the only commensal found. Studies were made on the biology of this animal and on its relationship with the host coral.

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METHODS

The coral to be collected was covered as completely as possible with one or more cloth bags while still in place, then broken off and returned to the laboratory for study. Placing the coral inside bags was awkward but necessary since many of the crabs would have escaped if the coral had simply been lifted from the water. At the laboratory dock, the pieces of coral were weighed and carefully examined while the cloth bags were rinsed in a bucket of water which was poured through a fine mesh screen. The crabs found on each colony were collected and measured. In addition, living crabs were studied both in nature and in the laboratory.

OBSERVATIONS AND CONCLUSIONS

Domecia acanthophora is a small crab with a mottled brown and cream carapace. Of 180 specimens examined, 162 were above 5.0 mm. in carapace breadth and easily identifiable as to sex, 58 being males and 104 females. The largest male had a carapace breadth of 15.0 mm. while the mean for males was 8.2 mm. For females the comparable figures were 14.0 mm. and 8.4 mm. The smallest ovigerous female had a carapace breadth of 5.6 mm.

The host coral

Three species of *Acropora* are known from the Caribbean (Wells, 1956) and all were found at Enrique Reef (Fig. 1). *Acropora cervicornis* (Lamarck) has branches up to 25 mm. in diameter and grows in large loosely branching colonies which would appear to offer the crabs very little shelter. About ten colonies were examined carefully in the water and crabs were indeed found to be quite scarce, with occasional individuals occurring at a fork or some other site which offered a little protection.

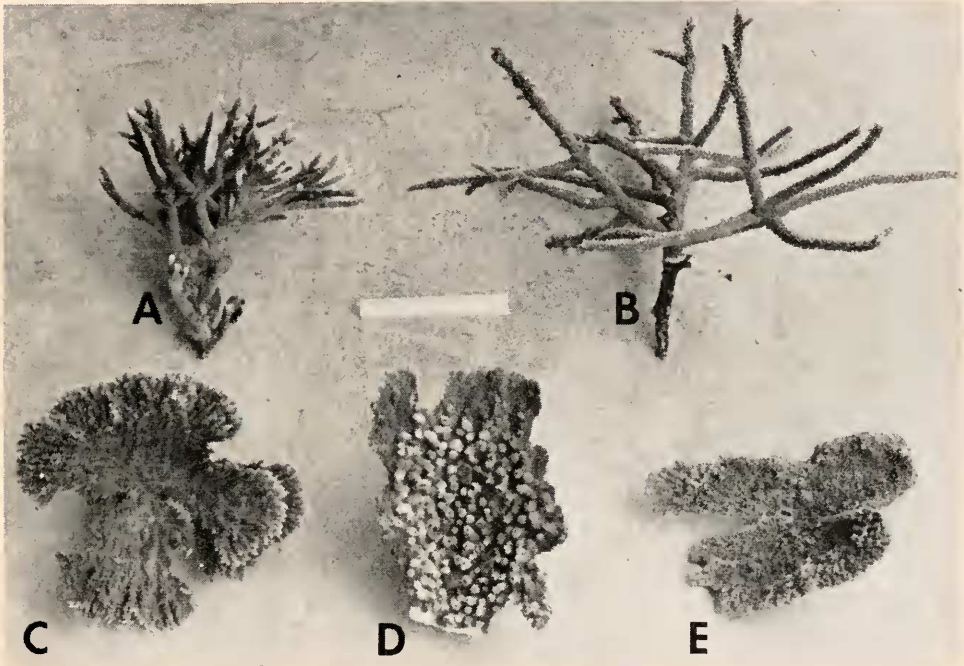


FIGURE 1. A, *Acropora prolifera*. B, *Acropora cervicornis*. C-E, *Acropora palmata*. C, A colony with considerable peripheral branching. D, A colony with considerable algal-induced vertical branching. E, A colony with little peripheral branching.

Acropora prolifera (Lamarck) is similar to the above species but has thinner, more closely spaced branches and forms thickets offering considerable shelter. The crabs seemed to have a patchy distribution, as certain regions of coral contained four or five crabs in a space of 25 cm.³, while much larger and apparently equally suitable regions had none at all.

Colonies of the third species, *Acropora palmata* (Lamarck), are much more massive than those of the preceding two, and typically consist of a central trunk with a number of flattened, horizontal sheets of coral spreading out laterally. These colonies range up to 6 feet in height and are very abundant on the La Parguera Reefs. The peripheral portions of the colony are usually branched to varying degrees but as new outward growth occurs, the spaces between the older

branches are filled in, forming a solid, central plate of coral. The peripheral branching was most delicate and extensive in small colonies in about eight feet of water in the channel off the western edge of the reef and seemed least developed in colonies on the seaward face of the reef. This observation is similar to that of Almy and Carrión-Torres (1963) who found small finger-like peripheral branches in colonies growing in the back-reefs. With regard to the central coral plates which compose the bulk of the colony, many are quite smooth while others show varying degrees of diagonal or vertical branching on the upper surface. These branches are generally quite short. An interesting type of vertical branch has a tuft of algae in the center (Fig. 1D). This extends down to the base of the branch and thus it seems likely that the plate was damaged in some way, allowing the algae to settle, and that the coral has grown up around it. On one occasion a coral plate was seen which contained round white spots where the coral tissue had been removed. These spots were grouped in a manner similar to that often found for the algae-tipped branches and were identified by Dr. Glynn as the work of the polychaete *Hermodice carunculata* (Pallas) (Marsden, 1962; Glynn, 1963). It would seem that algae could settle easily on the exposed spots and that polychaete predation may thus contribute to branch formation.

Acropora palmata contains relatively more specimens of *Domecia acanthophora* than do the preceding two coral species and was studied the most intensively. On examination it is seen that the great majority of crabs are not merely sheltering among natural features of the colony but instead are inhabiting structural deformations of the living coral, which, for lack of a better name, will be called "resting places." The term gall should perhaps be reserved for more regular deformations than those shown here. These resting places (Fig. 2) can be divided into three general types: crevices, pits and spaces between vertical branches. I believe that all of these types result from the response of the coral to the continuing presence of a crab.

A crevice is the most inclusive category and is simply a space between a branch and the adjacent coral. When a crab is removed from its crevice, it is seen that the coral has grown away from and around the crab, forming a shelter for it. In addition, the corallites in the region touched by the crab are either thickened and rounded off or absent altogether. Crevices are most common in colonies where much natural peripheral branching occurs and where they can be seen in all stages of development. They can also be found under diagonal branches. I feel that a crevice originates when a young crab settles in an available space and stays there long enough for the coral to be modified by its presence. As the coral continues to grow and the spaces between branches begin to be filled in, the two sides of the crevice may grow so that the crab comes to occupy a slit extending down into the colony. In some cases, the sides of the crevice will unite beyond the crab leaving a space extending from one side of the colony to the other.

Another and common alternative is that the crab will be surrounded on all sides but one by growing coral and the crevice then will be converted into a blind pit. The coral inside a pit is, of course, dead, while the opening is surrounded by a raised lip of corallite-free, living coral. These pits may be quite shallow or may extend well down inside the coral skeleton, depending on the degree to which the opening has remained in the region of active coral growth. Since Vaughan (1915)

has reported that *A. palmata* may increase in diameter as much as 95 mm. a year, it would seem that a well formed pit could develop in six months or less and that a rudimentary crevice could develop in a matter of weeks.

Crabs are also found sheltering between certain vertical branches and these spaces too are found to be modified. They are characterized by thickened corallites and a slightly deformed growth of the branches involved.

It can thus be seen that the suitability of a colony for resting place formation varies with the amount of diagonal, vertical and peripheral branching that it shows.

A further indication of the evident ease with which coral skeleton can be modified was provided by a colony of *Acropora palmata* in which the corallites were thickened in an area brushed by the seemingly light touch of the expanded tentacles

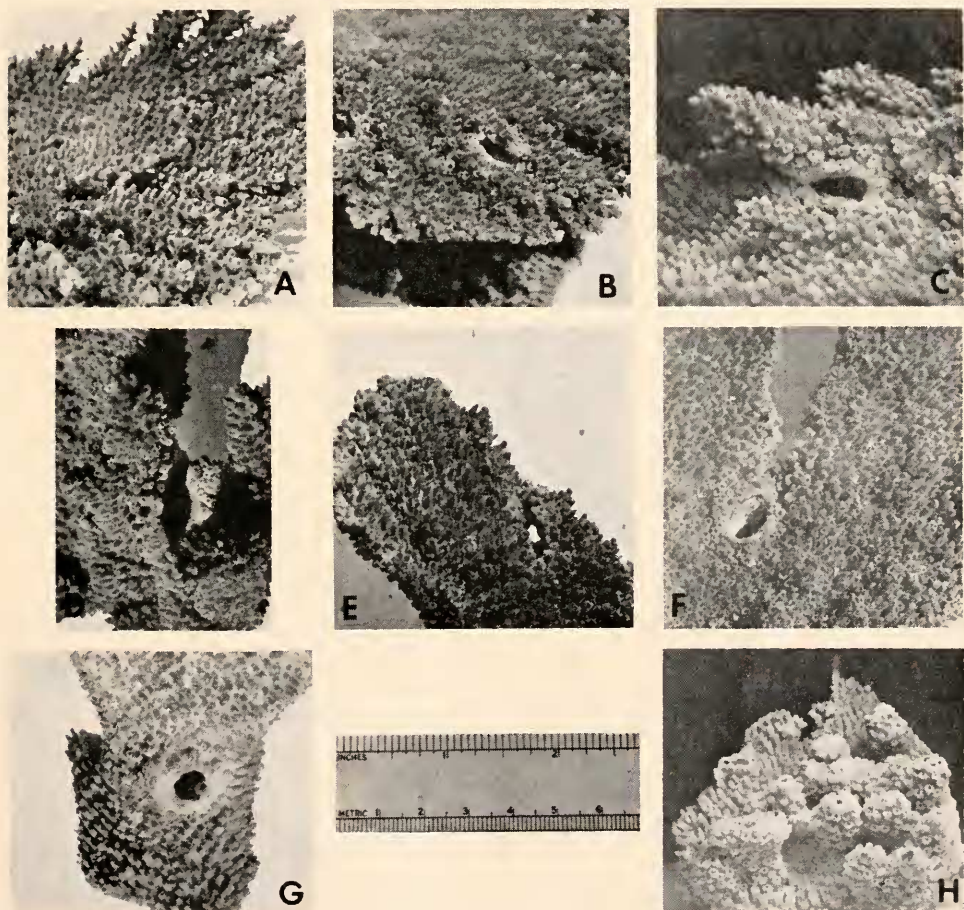


FIGURE 2. Modifications induced in *A. palmata* by *D. acanthophora*. A, Early stage of crevice formation in colony showing much peripheral branching. B, Older and better developed crevice in the same colony. C, Crevice under a diagonal branch. D, Well developed crevice at side of a colony. E, Crevice enclosed anteriorly. F, Pit. G, Pit. H, Modified space between vertical branches.

of an adjacent tube worm. The well known fact that many branching corals, including *A. palmata*, have different growth forms under different wave conditions (Wood-Jones, 1907; Vaughan, 1919; Storr, 1964) also shows that the deposition of coral skeleton can be much influenced by factors in the environment.

The above formation of resting places is not unique, as similar though more regular modifications are known to be induced in their coral hosts by the various gall-crabs of the family Haplocarcinidae. The best known species, *Haplocarcinus marsupialis* Stimpson has been well described by Potts (1915). Here the male is free-living while the female forms galls in branching corals of the family Pocilloporidae. The coral grows around the crab, eventually enclosing her except for several small openings in the top of the gall. Potts noticed a malformation of both corallites and polyps on the inside of the gall and regarded this and the growth of the gall itself as the reaction of the coral to the crab's respiratory currents. Although respiratory currents may play a part in resting place formation in *Acropora palmata* it seems more likely that the coral is responding to contact with the crab itself. This is particularly true in the case of crevices and the modified spaces between branches where the coral is altered in the region actually touched by the crab but not in the area in front of the crab against which the exhalant respiratory current must press.

The remaining members of the Haplocarcinidae form pits and crevices in various massive corals (Fize and Ser  ne, 1957). The only previously reported case of decapod modifying *Acropora* is that of the uncommon Indo-Pacific gall shrimp, *Paratypton siebenrocki* Balss.

The commensal

Domecia acanthophora looks much like any free-living xanthid crab and as evidenced by the individuals on *A. cervicornis* and *A. prolifera* is not dependent on the existence of a resting place. This is in marked contrast to the gall-crabs and gall-shrimp mentioned above which are very much modified structurally and are seemingly unable to survive outside of their galls for any length of time. Furthermore, *D. acanthophora* is not an obligate commensal of a particular group of corals. Rathbun (1930) reported it "among sponges and branches of corals and in holes of dead corals and stones" and mentioned the corals *Meandrina* and *Porites*. Rathbun (1921) found it on *Acropora* at Barbados. At La Parguera, Dr. P. W. Glynn (personal communication) found this crab commonly on *Acropora palmata* and in beds of *Porites furcata* in shallow water on reef flats.

The specimens of *D. acanthophora* observed on *Acropora* in nature moved very little. When disturbed, however, they could move very rapidly across the coral colony. Those inhabiting *A. palmata* were very reluctant to leave their resting places and generally would not do so until touched with forceps. In the laboratory crabs showed a strong negative phototaxis and a low thigmokinesis. These traits are of course shared by many benthic organisms. If there is competition among crabs for resting places, some type of territorial behavior might be expected. This was never observed.

Many colonies of *Acropora* showed no evidence of commensals and so were not collected. Table I shows the results of several collections that were made.

Note the fairly close correspondence which exists between the number of resting places found on *A. palmata* and the number of crabs on the colony. This may be due to predation of unprotected crabs by the many small fish which hover around the coral or more likely to the tendency of the crab to keep moving until it is adequately sheltered. The small excess of crabs over resting places may be due to (a) crabs wandering over the colony, or (b) crabs inhabiting structurally unmodified shelters, or (c) two crabs inhabiting the same resting place. The first two alternatives were noticed occasionally, the third only once. The vast majority of resting places seen in nature were found to be inhabited.

Some differences were noticed in the crabs found on the two species of coral. Of those shown in Table I, the largest taken from *A. prolifera* was a female of 10.1 mm. carapace breadth while *A. palmata* contained 5 males and 13 females of this size or larger. As can be seen from Table I the sex ratio is about equal in crabs inhabiting *A. prolifera* while on *A. palmata* there were twice as many females as males.

TABLE I
*Colonies and portions of colonies of Acropora collected from Enrique Reef
between July 20 and August 5, 1965*

	<i>A. palmata</i>													<i>A. prolifera</i>								
Colony number	1	2	3	4	5	6	7	8	9	10	11	12	13	1	2	3	4	5	6	7	8	9
males		3	2	5		5	1				5	4	1	1	1	4	1		2		1	2
ovigerous females	1	6	3	5	1	6	2				7	4	1	1	1		1	1	2	1	2	1
non-ovigerous females	1	4		5		2	1		1		4	3	1	2	1		1	2				
juveniles (under 5 mm.)				2		1	1	1			2	1		2			1		1			
Total	2	13	5	17	1	14	2	3	2	0	18	12	3	6	2	5	1	2	5	1	4	3
Number of resting places found on colony	1	10	4	14	1	11	1	3	2	0	16	7	3	0	0	0	0	0	0	0	0	0

To investigate the mobility of *D. acanthophora*, the resting places on several adjacent colonies of *A. palmata* were mapped and examined on 8 of the next 13 days. After each day's observation the crabs inhabiting the resting places were destroyed. The results, shown in Table II, permit several observations to be made. (1) Crabs do not have to make their own resting places, but will readily inhabit those they find vacant. Thus once a resting place is formed, it could be used by many crabs during the life of the colony. (2) There is evidently considerable movement of *Domecia* on to the colony and if the originally vacated resting places had been left undisturbed, they would probably all have been re-occupied in about a week. (3) Much of the movement involved smaller individuals. It would have been highly desirable to measure each crab, but unfortunately they were so agile or else so well entrenched they could not be caught without destroying them. (4) Some resting places are strongly preferred.

Feeding habits

Specimens of *D. acanthophora* kept in the laboratory would hardly move unless disturbed and refused to eat fragments of shrimp or fish. The main activities that were observed were flicking movements of the first antennae and periodic extensions and withdrawals of the second maxillipeds.

Most brachyuran crabs are carnivores or scavenging omnivores and their stomachs contain fragments of more or less identifiable animal or plant material. The stomachs of 14 *D. acanthophora* contained no animal organisms, no fragments of muscle, chitin or other tissue and only a very occasional strand of algae. The bulk of the material in the stomachs was a white, structureless mass containing variable amounts of large bacteria. Small mineral grains and sponge spicules were also commonly found. One crab contained many small yellowish cells about 10 microns in diameter which may have been zooxanthellae.

TABLE II

Re-inhabitation of various resting places on adjacent areas of A. palamata. All crabs were destroyed following each day's observations

		Day								
		1	2	3	4	7	8	9	11	14
Crevices	a	P	—	—	—	—	—	—	—	—
	b	P	—	L	M	M	—	M	S	M, S
	c	P	—	—	—	—	—	S	—	—
	d	P	P	—	M	—	—	—	—	—
	e	P	—	—	—	S	—	—	—	—
Pits	A	P	P	S	S	—	—	S	S	—
	B	P	P	—	—	S	—	—	—	—
	C	P	P	S	—	—	—	—	—	—
	D	P	P	S	S	—	—	S	—	—
Spaces between vertical branches	1	—	—	—	—	—	—	—	—	—
	2	P	P	—	—	—	—	—	—	—
	3	P	—	P	—	M	—	S	—	—
	4	—	—	—	—	—	—	—	—	—

S, M, L = small, medium or large sized crabs

P = crab present, size not noted

— = no crab present

The mouthparts of two fairly typical non-commensal crabs, the shore crab, *Carcinus maenas* and a spider crab, *Hyas coarctatus*, are very similar even though the crabs belong to different superfamilies (Borradaile, 1922; Hartnoll, 1963). When the mouthparts of *D. acanthophora* (Fig. 3) are compared with those of the above crabs, however, a number of marked differences can be seen. (1) The dactyl of the third maxillipeds of *Domecia* has a much longer tuft of terminal hairs. (2) The armature of the dactyl of the second maxillipeds is very different. In *D. acanthophora* the dactyl is considerably broadened and bears many stout setae on its inner surface. These are arranged in rows with each row being composed of setae of a different length. The longest ones are the most ventral, above which are rows of progressively shorter and more dorsal setae. On either side of the terminal portion of each seta there is a row of up to 12 lateral bristles. Each seta ends in a peculiar tripartite paddle which turns upwards at a right angle. This paddle is composed of the tip of the seta and a thickened bristle on either side. The longer setae curve dorsally and have a greater number of lateral bristles than

do the shorter ones. (3) The first maxillipeds and second maxillae have better developed setae on their medial surfaces. (4) The mandibles are more weakly calcified while the mandibular palp has a different shape and fewer setae.

The teeth of the gastric mill also differ from those found in typical brachyurans. In ten species of spider crab, Hartnoll (1963) found that the lateral teeth of the

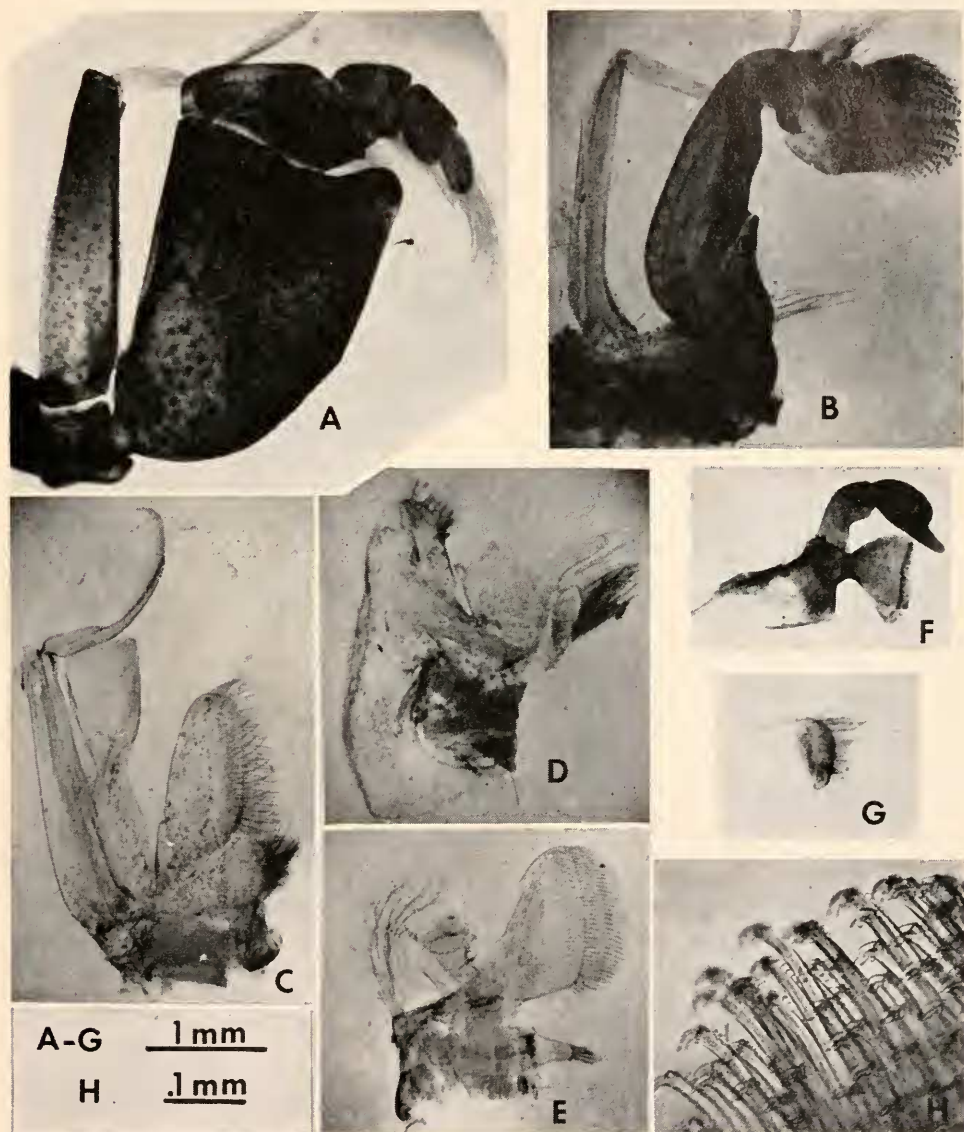


FIGURE 3. A-G, Ventral view of right mouthparts of female *Domecia acanthophora*, 12.4 mm. carapace breadth. A, Third maxilliped. B, Second maxilliped. C, First maxilliped. D, Second maxilla. E, First maxilla. F, Mandible. G, Paragnath. H, Dorsal view of spines on distal end of the dactyl of the second maxilliped.

zygocardiac ossicles had from 3-7 cusps and from 0-7 ridges. In *Carcinus* they have 5 fairly blunt cusps and 8 ridges (Potts, 1915). In *D. acanthophora*, however, the lateral teeth consist of 13-16 fairly slender cusps whose points vary from rounded to sharp and about 20 ridges.

In the light of the above observations it is probable that *D. acanthophora* removes its food from the water with the second maxillipeds. It is not a typical filter-feeder, however. The only possible filtering structure is the dactyl of the second maxillipeds and this is of relatively small size and lacks the abundant pinnate setae usually found in the filter of filter-feeding crustaceans (Marshall and Orr, 1960). The dactyls of ten crabs were carefully examined and although the crabs had not been preserved until an hour after being caught, in nine cases the setae contained amorphous material with inclusions of sand grains. In two cases, the setae were largely covered with a sheet of this material while in the others small pieces were entangled on some of the paddles. There were a very few small particles on the setae which did not seem to be in a matrix of other material. This material is very similar to that found in the stomach and is doubtless scraped off the dactyl by the setae on the medial surfaces of the first maxillipeds and second and first maxillae, and placed between the protruding mandibles.

A likely source of this amorphous material is the organic detritus drifting in the water since descriptions of it agree closely with the stomach contents. Hunt (1925) describes detritus from Plymouth as a pale brown flocculus containing living micro-organisms, fragmented skeletal parts and sand grains. Riley (1963) states that (p. 273) "organic aggregates in Long Island Sound commonly consist of pale yellowish or brownish amorphous matrices with inclusions of bacteria, silt particles and sometimes phytoplankton." Coral mucus is also a possible source of the material eaten by *D. acanthophora*. It is shed abundantly by *Acropora* and could contain sand grains and spicule fragments which settle on it. I doubt if it is a major food, however. Crabs were never observed to eat mucus and do not seem to move around the colony as they might if they were collecting it. One crab was seen to remove a strand of mucus that had drifted into its mouthparts.

ZOOGEOGRAPHY

The genus *Domecia* occurs in tropical coral habitats around the world and contains three species. The best known is *D. hispida* Eydoux and Souleyet. It extends from the Red Sea across the Pacific to the west coast of America and is apparently restricted to colonies of *Pocillopora*. The stomach contents of a specimen of *D. hispida* from the Galapagos were identical to that reported above for *D. acanthophora*. The mouthparts of this specimen were very similar to those of *D. acanthophora* and the two species doubtless have the same feeding habits. Although *Hapalocarcinus* forms galls in *Pocillopora*, deformation of this coral by *D. hispida* has not been reported.

The second species, *D. glabra* Alcock, extends across the Indo-Pacific from Madagascar to Tahiti and has been taken from *Acropora* (Garth, 1964; Patton, 1966). Resting place formation has not been reported but may occur on the plate-forming species.

As to the third species, Guinot (1964) has shown that specimens of *Domecia* from the tropical Atlantic do not represent *D. hispida* as previously supposed but

constitute a distinct, though very similar species, *D. acanthophora* (Desbonne and Schramm). Furthermore, the American specimens *D. acanthophora* forma *acanthophora*, which occur from South Carolina to Brazil, can be distinguished from African specimens *D. acanthophora* forma *africana* Guinot. Little is known of the habitat of the African form except that it is found among corals.

The genus *Acropora* is very well developed in the Indo-Pacific and has quite a varied fauna of commensal decapods (Garth, 1964; Patton, 1966). The types with fairly close branches have the most commensals but even species similar to those of the Caribbean have more than one commensal species. The question then arises as to why *Domecia acanthophora* is the only decapod commensal with Puerto Rican *Acropora*. The answer may well be an historical one. The present-day hermatypic Atlantic corals are believed to result from a time when the Tethys Sea connected the Atlantic with the Indian Ocean. This connection was permanently broken in the Miocene. Later in the Tertiary the families Acroporidae and Pocilloporidae had an enormous development in the Indo-Pacific (Wells, 1956), producing numerous species, many of which offer a great deal of shelter to commensals. It seems likely that the development of the present extensive commensal faunas of these two families would have followed or paralleled this expansion of their hosts. If this was so, the *Acropora* fauna which evolved in the Indo-Pacific would have had no opportunity to reach the Caribbean. There is no record of *Acropora* occurring in the East Pacific (Durham and Allison, 1960) and the only possible tropical connection between the Indo-Pacific and the Atlantic would have had to involve the East Pacific and a Central American waterway.

Pocillopora, on the other hand, though absent in the Caribbean since the Miocene (Durham and Allison, 1960), is common in the East Pacific and contains several of the typical Indo-Pacific *Pocillopora* commensals including abundant *Domecia hispida* (Crane, 1947; Garth, 1948). The last Central American seaway was closed either in the late Miocene (Durham and Allison, 1960) or the Pliocene (Lloyd, 1963). Although the first record of *Pocillopora* in the East Pacific is in the Pleistocene (Durham and Allison, 1960), it may have been there earlier along with its commensals and prior to the closing of connections with the Atlantic. If this was the case, then *D. hispida* could have crossed over and established itself on Atlantic *Acropora*. The ability of *Domecia* to feed on detritus could have been sufficient reason for it being the only one of the *Pocillopora* commensals to successfully cross into the Atlantic and transfer to a new host. Following the separation of the two oceans, the Atlantic *Domecia* would have evolved into a separate species.

An alternative explanation for the presence of *Domecia* in the Atlantic is that the genus is older than the other commensal decapods and evolved before the severing of the Tethys connection. This seems less likely since the great morphological similarity of *D. hispida* and *D. acanthophora* suggests that they have a relatively recent common ancestry.

SUMMARY

1. The xanthid crab *Domecia acanthophora* was collected from three species of the coral *Acropora* at Enrique Reef, La Parguera, Puerto Rico.

2. The commensal was most commonly found on the flattened coral sheets of *Acropora palmata*. Here the majority of crabs inhabit various types of structural deformation of the coral which are called resting places. These are believed to be formed by the growth of the coral around and to some extent away from a resting crab.

3. Although undisturbed crabs remain quite motionless, ones which are disturbed are capable of rapid movement over the colony. There is at least some movement of crabs around the reef as vacated resting places will be re-occupied by new crabs.

4. The mouthparts of *D. acanthophora* differ from those found in typical crabs. In particular, the mandible is weakly calcified and the second maxilliped possesses rows of peculiar paddle-tipped spines on the distal margin of the dactyl. The most likely food for the animal seems to be organic detritus which it separates from the surrounding water.

5. The genus *Acropora* harbors numerous commensal decapods in the Indo-Pacific but apparently only one in the Caribbean.

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